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Distribution patterns of native freshwater fishes in Patagonia (Argentina)

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Abstract

The Patagonian ichthyofauna comprises a total of 29 species. This low species richness contrasts with other cold-temperate regions of the southern hemisphere. The fauna includes only 15 species native to the Patagonian Province and seven to the Brazilian Province. Knowledge of native fish fauna diversity patterns is still fragmentary. Based on extensive sampling during the IBOY initiative and also reviewing seminal and review literature, we provide an updated perspective of native freshwater fishes in Patagonia by describing and analyzing their distribution and occurrence across basins.

The results show that species richness varies along latitude, with a maximum at the 38°–40° interval, principally due to the presence of Brazilian species inhabiting northern Patagonia. However, species numbers remained constant south of 48° latitude. We report extended distribution ranges for several species such as *Diplomystes mesembrinus, Hatcheria macraei, Trichomycterus areolatus,* and *Odontesthes hatcheri*, and also the new discovery of a Brazilian species *(Corydoras paleatus)* in the north of Patagonia. Cluster analysis based on presence-absence information revealed co-occurrence patterns at the level of basins, showing that only few species (*Percichtys trucha, Odontesthes hatcheri, Hatcheria macraei, Galaxias platei*, and *G. maculatus)* are ubiquitous. Restricted distribution and even endemism for the remaining species could be attributed to river drainage systems which influence dispersion ability, to the influence of past glaciation events, and impact by introduced salmonids in the last century. Future research therefore should be focused on distribution patterns of introduced species since they are an important component of present Patagonian fish assemblages. Also, efforts should be devoted to understanding how diversity patterns of freshwater fish communities vary across scales and how community changes are relevant for native species conservation.

Key words: Native species, Patagonia, diversity, distribution, habitat, presence-absence

See also Electronic Supplement at **http://www.senckenberg.de/odes/03-07.htm**

Introduction

The Patagonian ichthyofauna exhibits low species richness (Ringuelet 1975, Arratia et al. 1983) which contrasts with other cold-temperate regions of the southern hemisphere. Most previous studies on native species have focused on trophic, reproductive and taxonomic features (see Ferriz et al. 1998 for a review), but almost no attempts have been devoted to distribution and diversity patterns at a broad spatial scale. Quirós et al. (1986), for example, presented information on several lake communities but based their results on fisheries studies which may be biased by gear selection. In turn, Arratia et al. (1983) and Bello (2002) provided information on native species distribution but mostly for large rivers (Negro, Limay, Neuquén, Santa Cruz, Senguerr, Colorado, Deseado, etc).

During the last years there has been increased concern for the conservation status of native species. Stocking of exotic salmonids in Patagonian lakes and rivers began in 1904 (Baigún & Quirós 1985) and has been identified as a potential source of impacts. Also, it is not well known how environmental conditions are related to species distribution, and how exotic species have interacted and modified the community structure in different basins. Bertonatti & González (1992) and Chebez (1994) specu-

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lated that almost 50% of the native species may have been affected by conservation problems, and Bello & Ubeda (1998) suggested that nine of the native species could be endangered. Such results reinforce the concept that distribution and diversity information is critical to the development of conservation tools.

The BIOPAT Project (Biodiversity of Freshwater Fish in Patagonia), as part of the International Biodiversity Observation Year (IBOY) initiative, is an attempt to update and increase the knowledge of native fish fauna diversity. Such information is necessary to provide a conceptual framework to define the status of species and to preserve and restore natural biodiversity in Patagonian freshwater ecosystems. Although over the last few years there has been an increase in studies of fish biology in Patagonia, a biodiversity approach is necessary to assess impacts from damming, deforestation, land use, water diversion, and species introductions.

In this study we provide an updated perspective on a broad geographical scale of native freshwater fishes in Patagonia by describing and analyzing their distribution patterns across basins. Such analyses represent an effort to identify information gaps on species distribution and provide guidelines for further research efforts in order to acquire appropriate information for preserving Patagonian fish diversity.

Study area

Patagonia is a large territory that occupies the southern part of Argentina including the Provinces of Tierra del Fuego (and neighboring islands), Santa Cruz, Chubut, Río Negro, Neuquén, and also the southeastern part of Buenos Aires Province. This region is bordered by the Andes to the west, the Atlantic Ocean to the east, and by the río Colorado to the north (Fig. 1). Past glaciations shaped the landscape until the end of the Pleistocene (Ashworth & Hoganson 1993), creating lakes and rivers after the glaciers melted, particularly in the Andes (Auer 1958). Lakes located on the plateau but not in the Andes are mostly of tectonic and eolic origin (Iglesias de Cuello 1982). Volcanism also had a strong influence, and lakes located in the Andes/plateau ecotone were filled with ashes (Marcolini et al. 1998). Because soil composition is diverse, ionic qualities are distinct among the basins. Oligotrophic lakes are very common in the Andes, whereas more eutrophic and saline lakes are more common on the plateau (Baigún & Marinone 1995). Climatic characteristics are very heterogeneous, particularly along a west-east axis. Most of the moisture carried by southern Pacific winds is removed by the orographic effect of the Andes mountains, defining a noticeable environmental gradient at the Argentine slope that influences overall distribution of the biota (Veblen & Lorenz 1988). Patagonian hydrology is characterized by the presence of several large and long rivers crossing the territory from the west to the Atlantic Ocean. However, some rivers cross the Andes and reach the Pacific slope. Moreover, there are several large lakes that are shared by Argentina and Chile and have outlets both to the Pacific and Atlantic oceans. In northwestern Patagonia several dams have been constructed, particularly in the Limay and Neuquén river basins, that have resulted in the formation of several very large reservoirs (up to 800 km^2).

The fish community

The Patagonian ichthyofauna belongs to the Austral biogeographic region which in turn encompasses the Patagonian and Chilean ichthyogeographic provinces (Ringuelet 1975, Arratia et al. 1983). The Patagonian Province is borded to the north by the Parano-Platense and Andino-Cuyana Provinces. The Patagonian freshwater ichthyofauna comprises 29 species, but only 15 of these are native (Table 1). These numbers could be even

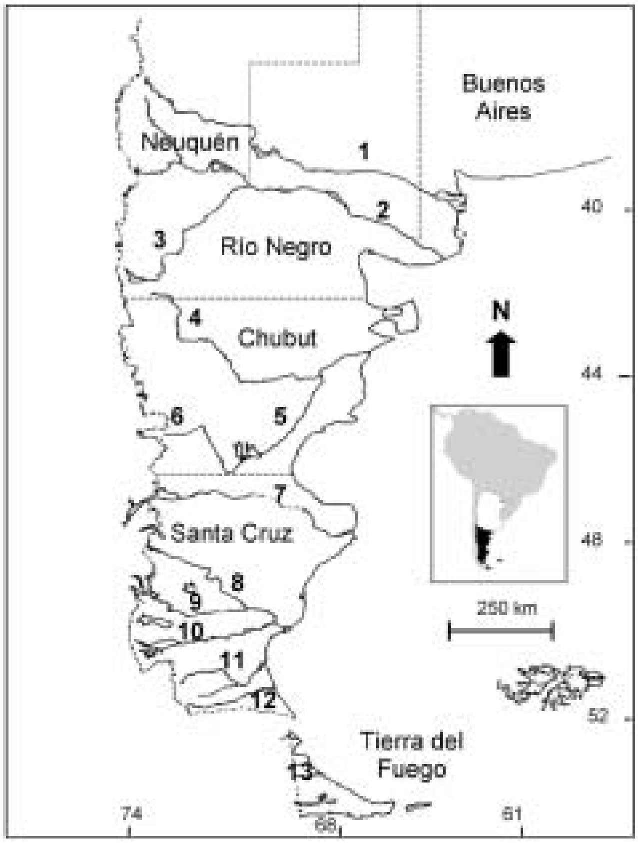

Fig. 1. General map of Argentine Patagonia, showing provinces and main rivers (numbered in boldface): 1 Colorado River, 2 Negro River, 3 Limay River, 4 Chubut River, 5 Chico River, 6 Senguer River, 7 Deseado River, 8 Chico River, 9 Chalia River, 10 Santa Cruz River, 11 Coyle River, 12 Gallegos River, 13 Grande River.

lower if the taxonomy of Percichthyidae were better understood. For example, Lopez Albarello (1999) claimed that *Percichthys altispinnis* and *P. vinciguerrai* should not be considered as separate species.

Arratia et al. (1983) noted that the Chubut River represents the true limit for the typical Patagonian fish fauna, because Brazilian species had never been reported south of this river. However, Brazilian and Patagonian species merge along the Negro and Colorado basins, defining a wide zoogeographic transition zone recognized as an ecotone (Almirón et al. 1997).

Patagonian fish species have been described as being restricted in distribution. Species such as *Percichthys altispinnis*, *Aplochiton taeniatus*, *Aplochiton zebra*, *Diplomystes viedmensis* and *D. mesembrinus* have been reported from only a few lakes and rivers, but information is still fragmentary. *Gymnocharacinus bergi* represents a unique case of extreme endemism (Ringuelet 1975, Menni & Gómez 1995, Ortubay et al. 1997). On the other hand, the fauna also comprises six exotic species, including rainbow trout (*Oncorhynchus mykiss*), chinook (*Oncorhynchus tschawytscha*), brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), lake trout (*Salvelinus namaycush*), landlocked salmon (*Salmo salar sebago*), and common carp (*Cyprinus carpio*), of which the rainbow trout exhibits the widest distribution (Baigún & Quirós 1985). In the last decades, *Oncorhynchus tschawytscha* has entered through Pacific drainages, such as the Corcovado (Grosman 1992) and Pico rivers (first author's observ., 2000), and developed stable populations. Unlike in Chile and New Zealand, most of the Patagonian salmonids are not anadromous. Only the above-mentioned chinook populations, the steelhead stock from the Santa Cruz River, and brown trout populations inhabiting the Deseado and Grande rivers have developed migratory habits in Atlantic-slope rivers.

Table 1. Native and exotic freshwater fish species inhabiting lotic and lentic environments in Patagonia. Asterisks (*) denote species of Brazilic origin (Parano-Plata Province).

Order	Family	Scientific name	Status
Salmoniformes	Salmonidae	*Oncorhynchus mykiss* Richardson, 1836	exotic
		Oncorhynchus tschawytscha Walbaum, 1792	exotic
		Salmo trutta Linné, 1758	exotic
		Salmo salar sebago Girard, 1855	exotic
		Salvelinus namaycush Walbaum, 1792	exotic
		Salvelinus fontinalis Mitchill, 1815	exotic
Osmeriformes	Galaxiidae	*Galaxias maculatus* Jenyns, 1842	native
		Galaxias platei Steindachner, 1898	native
	Aplochitonidae	*Aplochiton zebra* Jenyns, 1842	native
		Aplochiton taeniatus Jenyns, 1842	native
Perciformes	Percichthyidae	*Percichthys colhuapiensis* MacDonagh, 1955	native
		Percichthys vinciguerrai Perugia, 1891	native
		Percichthys trucha Cuvier & Valenciennes, 1840	native
		Percichthys altispinnis Regan, 1905	native
Cypriniformes	Cyprinidae	*Cyprinus carpio* Linné, 1758	exotic
Cyprinodontiformes	Anablepidae	*Jenynsia multidentata** Jenyns, 1842	transplanted?
	Poeciliidae	*Cnesterodon decenmaculatus* Jenyns, 1842	transplanted?
Siluriformes	Diplomystidae	*Diplomystes mesembrinus* Ringuelet, 1984	native
		Diplomystes viedmensis MacDonagh, 1931	native
		Diplomystes cuyanus Ringuelet, 1965	native
	Trichomycteridae	*Hatcheria macraei* Girard, 1855	native
		Trichomycterus areolatus Arratia & Chang, 1975	native
	Callichthyidae	*Corydoras paleatus** Lacepede, 1803	transplanted?
Atheriniformes	Atherinopsidae	*Odontesthes bonariensis** Cuvier & Valenciennes, 1835	transplanted
		Odontesthes hatcheri Girard, 1885	native
Characiformes	Characidae	*Oligosarcus jenynsii* Günther, 1864	native
		*Gymnocharacinus bergi** Steindachner, 1903	native
		*Astyanax eigenmanniorum** Cope, 1894	native
		*Cheirodon interruptus** Jenyns, 1842	native

Material and methods

Samples were taken in the years 2000 and 2002 within an extensive program developed for Patagonian lakes and rivers as part of the BIOPAT project. Sampling covered all Patagonian Provinces and mostly focused on small lakes and low-order streams whose fish fauna was unknown or incompletely recorded. In total, 18 lakes with a mean surface area of 250 hectares were sampled, and 46 sites on several Patagonian rivers. Additional information was obtained from seminal publications on fish distribution and zoogeographic analysis. We also revised material from the Museo de Ciencias Naturales "Bernardino Rivadavia" (MACN) collection, which is the most complete for Patagonian fishes.

Experimental fishing in lakes was performed by floating and bottom monofilament gill net and floating and bottom multifilament gill-net gangs. Floating gill nets were set at the shore, whereas bottom gill nets were set at the slope boundary with the lake bathyal zone. Mesh sizes were 21, 25, 30, 35, 39, 52.5, 60, 70, and 85 mm. Each net was 25 m in length at variable depth (2–4 m), with total gang lengths of 900 m. Fishing effort varied from one to two nights depending on lake area.

In low-order streams electrofishing was conducted with portable equipment, three electrofishing removals were performed in several reaches. At each sampling site, 3 to 5 reaches of 50 m length were selected according to the methods of Maret et al. (1997). This distance can be considered as the minimum length for detecting most species in pools and riffles (Stoneman & Jones 2000). For intermediate-order streams, we sampled a length equivalent to 20 times the mean width of the wetted channel. When possible we attempted to separate the sampled reaches in order to cover most of the environmental heterogeneity as represented by riparian vegetation, flow velocity, substrate, macrohabitat diversity, morphometric features, etc. In large rivers with high flow, electrofishing was performed only in shallow bays and backwaters.

Data analysis was based on a matrix constructed for presence/absence of species recorded for lentic and lotic environments, respectively. Details of this information can be found in the accompanying Organisms Diversity and Evolution Electronic Supplement (ODES 03-07, Tables A–V). Each of the 54 drainages identified on 1:100.000 or 1:250.000 scale maps was allotted a sample site. These drainages form the main tributary watersheds of large Patagonian rivers such as the Limay, Colorado, Chubut, Negro, Santa Cruz, etc., or they drain to the Pacific Ocean, or form endorrheic basins. The large rivers were divided into low, middle and upper sections between which we hypothesized the fish assemblages to vary. Marine sites and waterbodies located on small islands were disregarded in this analysis.

Association of species co-occurrence at the defined drainages was examined by using average-linkage cluster analysis and the Sørensen similarity index, which doubles weights for co-occurrences (Romesburg 1984).

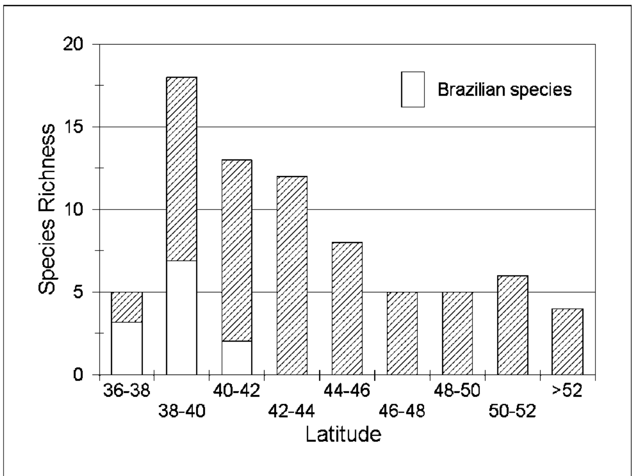

Fig. 2. Variation of species richness along latitude.

Results

Through the extensive sampling program we found 9 of 14 fish species reported from Patagonia. Based on total matrix entries, 41% were referred to lotic waterbodies, 53% to lentic environments, and 18% to reservoirs. For lotic environments, we found that most of the historical sampling efforts had been concentrated on large rivers, with 43% corresponding to the Negro, Limay and Neuquén rivers. Only 8% of the information was available from low-order rivers.

Species richness varied with latitude, the maximum number of species was found in the 38°–40° interval (Neuquén-Río Negro Provinces; Fig. 2). Species richness decreased to the south, but remained almost constant south of 48°. The influence of Brazilian species at northern latitudes was also evident. When such species were removed from the analysis, species richness did not change substantially with latitude.

Based on literature data and our own samples, we developed updated distribution maps for each of the species (Electr. Suppl. 03-07, Figs A–I). In the genus *Diplomystes* (Electr. Suppl. 03-07, Fig. A), we could add the middle Chubut River to the distribution range of *D. mesembrinus*, an important new finding. Azpelicueta (1994b) considered that this species only develops small populations, and very few specimens have been collected during the last years. *D. viedmensis* appeared mostly distributed in lotic water bodies of the Limay watershed, *D. cuyanus* is found only in the Colorado River which separates the Patagonian and Andino-Cuyana zoogeographic provinces.

Our samples also show an extended geographic range for the Trichomycteridae family (Electr. Suppl. 03-07, Fig. B). We found *Hatcheria macraei* in the upper Neuquén River (Manzano Amargo and Andacollo), whereas *Trichomycterus areolatus* was detected in a tributary of the upper Chubut River (Lepa Creek). The latter species was also captured in the Ecker River, ex-

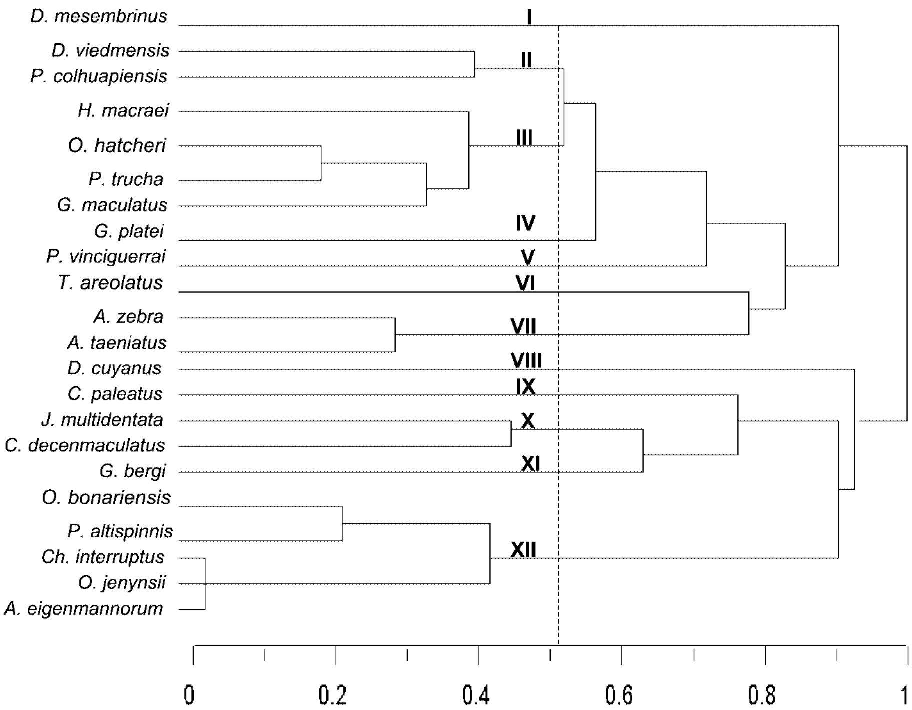

Fig. 3. Dendrogram of fish species association for identified watershed units derived from average-linkage clustering and Sorensen association index. Vertical dashed line represents cut level analysis (see text).

tending its distribution towards the plateau of southern Patagonia.

Brazilian species were restricted to the Colorado and Negro river basins (Electr. Suppl. 03-07, Fig. C), with the exception of *Gymnocharacinus bergi* which is known to be endemic to the Somuncura Plateau. The finding of *Corydoras paleatus* in the lower Limay River represents an important novelty, increasing Brazilian species richness in northern Patagonia. The northern distribution range for *Odontesthes hatcheri* is also expanded by finding this species in the upper Neuquén River and in the upper Epulaufquen and Vaca Laufquen Lakes (Electr. Suppl. 03-07, Fig. D).

The family Galaxiidae showed a very wide distribution across Patagonia, although the two included species have never been reported from the upper Neuquén basin and *G. platei* is absent from the northeast of Patagonia. (Electr. Suppl. 03-07, Figs E, F).

Geographical distribution in the family Percichthyidae differed between species (Electr. Suppl. 03-07, Figs G, H). For example, *Percichthys altispinnis* exhibited a very restricted distribution, and *P. colhuapiensis* was completely absent from Andean lakes. On the other hand, *P. trucha* appears to be ubiquitous, and we can extend its northern distribution range to several lakes belonging to the upper Neuquén basin (Electr. Suppl. 03-07, Fig. H).

For the family Aplochitonidae we can confirm the narrow distribution area mostly limited to the Futaleufu River basin, which is connected to the Pacific Ocean (Electr. Suppl. 03-07, Fig. I).

Whereas maps portray general distribution characteristics such as areas of concentration and boundaries, they do not easily display simultaneous association patterns. Cluster analysis of species co-occurrence in different catchments allowed the identification of up to 12 species groups at moderate similarity level (Fig. 3). Some of these consist of a single species, implying unique distribution characteristics (groups I, V, VIII, X, XI). Group III comprises ubiquitous species which are found in most of the main river basins across Patagonia. Groups II, IV, VI and VII reflect those species restricted to or reported from particular subbasins. Group XII mostly includes Brazilian species restricted to north Patagonia, and group X those that also occupy the Somuncura plateau.

Discussion

Fish species richness in Patagonia appears rather low compared with other cold-temperate regions in the southern hemisphere, even when Brazilian species are considered part of the fauna. McDowall (1978), for example, reported 27 native species for New Zealand and a total including exotics of 47 species. Brazilian species restricted to the northern area in Patagonia represent a distinctive feature comprising at present 30% of species richness.

The latitudinal range between 38° and 42° (Neuquén and Río Negro provinces), which includes the ecotonal area between the Patagonian and Parano-Platense zoogeographic provinces, appears to have the greatest species diversity due to the influence of Brazilian species. Almirón et al. (1997) reported new findings of Brazilian species in the last years, and Baigún et al. (2002) speculated that species such as *Jenynsia multidentata* and *Corydoras paleatus* could colonize northern Patagonia due to their tolerance for cold temperatures and saline conditions.

A high species diversity may be also related partially to the hydrographic characteristics in north Patagonia. Long rivers flowing westwards from the Andes exhibit higher discharges than those located in southern Patagonia and may facilitate species dispersion and colonization. The upper Limay River receives large tributaries from watersheds (e.g. the Alumine-Collón Cura system) which follow a north-south direction, connecting lower-order rivers and several lakes. A similar pattern is observed in the upper Neuquén River and its main tributary system, the Varvarco watershed. Such longitudinal systems, almost absent in southern Patagonia, may play an important role by connecting various waterbodies and enhancing the dispersal ability of several different species across basins.

The fossil record of southern South American fish assemblages in the Palaeozoic, Mesozoic and Cenozoic periods shows important differences (Arratia & Cione 1996). The present low species richness and disrupted distribution of the Patagonian fish fauna appears to be strongly related to large-scale geological events such as the Andes uplift during theTertiary, and was also shaped by Pleistocene-Holocene glaciation and volcanism (Mercer 1984). Glaciers modified native fauna distribution patterns on all levels (Markgraf 1985). Yet, the present distribution of Brazilian species is probably the result of increasing aridity during the Tertiary and of change in climatic conditions during the Pleistocene, narrowing their distribution ranges (Ringuelet 1975). The presence of the relict monotypic species *Gymnocharacinus bergi*, inhabiting the headwaters of Valcheta Creek on the Somuncura plateau, and reports of a few other Brazilian species such as *C. decenmaculatus* and *J. multidentata*, suggest that these species had a wider distribution in the past (Menni et al. 1996). The Andes uplift isolated fish populations on both sides of the mountain range (Cione 1979), as evidenced by, e.g., *Percichthys* and *Diplomystes* species. However, both taxa were well represented in South America before the Cenozoic, suggesting a broader distribution in the past. The diversification of *Percichthys* started in the Miocene, whereas fossil *Diplomystes* have been found in Cretacean deposits (Arratia & Cione 1996). Because siluriforms have an old evolutionary history and expanded during the late Cretaceous (Cione & Lafitte 1980), it is not surpirsing that some species survived the large-scale geological events, recolonized after Pleistocene glaciations, and now show ubiquitous distribution (e.g. *Hatcheria*).

On the other hand, the ability of species such as galaxiids to colonize the freshwater environment from the ocean after glaciers retreated could explain their broad distribution in Patagonia. Pacific river watersheds may have played an important role in fish dispersion on both sides of the Andes. In the past, members of *Galaxias* could have circumvented the geographic barrier imposed by the Andes by using these Pacific drainages, as hypothesized by McDowall (1971) and Gosztonyi & McDowall (1974). Our discovery of *G. platei* in small lakes belonging to the Pico River basin, which drains to the Pacific Ocean, supports this hypothesis.

We recognize that poor knowledge of the distribution of some native species may be also related to uneven historical sampling efforts in many basins. For example, we noted significant gaps in the distribution of *Galaxias maculatus* in vast areas of the Chubut and Santa Cruz provinces, and *Percichthys vinciguerrai* also showed discontinuous presence. Because the BIOPAT project has expanded the knowledge of their geographical range for various species and allowed us to discover yet another Brazilian species in northern Patagonia, we suggest that distribution limits for several species are still not well known. This is evidenced not only by range expansions for species on north-south axes, but also in an east-west direction, as shown by the finding of *Hatcheria macrei* in the Ecker River at the boundary of the plateau. Since Patagonia exhibits a strong limnological gradient on a west-east axis (Baigún & Marinone 1995), it is not surprising that new distribution patterns are found, driven by this noticeable ecological gradient.

An uneven species distribution pattern has important consequences for developing conservation criteria for native species and management guidelines for salmonids. If several native species are habitat-specific and probably have limited dispersal ability, introduction of exotic species may increase the potential for population reduction. The limited distribution of several native species cannot be dissociated from potential impacts by salmonids, which were heavily stocked during the last century (Baigún & Quirós 1985). An open debate remains about the impact of such species, and the controversy is relevant not only due to predation effects, but also to decreased survival rates as a result of habitat displacement. Predation on native species by introduced salmonids is well-documented in other southern hemisphere environments such as Australia and New Zealand (e.g. Crowl & Townsend 1992, McIntosh 2000). Habitat segregation in galaxids after the introduction of salmonids has been noted in small rivers of Australia (Jackson 1981), Tasmania (Ault & White 1994), and New Zealand (McDowall 1990, Minns 1990).

Macchi et al. (1999) suggested that the spatial heterogeneity characteristics of Patagonian large lakes and reservoirs allowed for better partitioning of resources, decreasing predation and competition among native and exotic species. Whereas some species, such as *Galaxias* sp., *Odontesthes hatcheri* and *Percichtys trucha*, appeared broadly distributed even after almost 100 years of salmonid stocking, suggesting minor impacts, *Diplomystes mesembrinus, D. cuyanus, Aplochiton taeniatus* and *A. zebra* show more restricted distribution ranges. We argue that small oligotrophic lakes and low-order rivers offer the most unfavorable conditions for salmonid introductions due to lack of suitable refuges and limited food supply, which may increase piscivory.

Developing sustainable management criteria for Patagonian fish communities requires an holistic perspective encompassing watershed connectivity, presence of critical habitats, distribution and abundance of native and exotic species, and also socio-economic demands and priorities. There are still some sub-basins and small high-altitude lakes in Patagonia that appear to be free of salmonids. These environments represent probably the last opportunity to understand ecological features of natural, balanced native fish communities, and could serve as a valuable reference for comparison with impacted watersheds inhabited by salmonids.

Future work in Patagonia should address and elucidate how diversity patterns of freshwater fish communities vary across spatial scales (e.g. α-, β- and γ-diversity) and how these characteristics are linked and can be applied in biodiversity conservation. Such studies should incorporate information on introduced salmonids as some species have demonstrated successful acclimatization and represent an important component of current fish assemblages. The existing management paradigm based on achieving sustainable fisheries or fish yield mostly based on salmonid status should be replaced by a new criterion based on achieving sustainable fish communities. This approach should incorporate the importance of native species. Such a policy would require defining also protected salmonid-free areas, creating sanctuaries, and even reducing salmonid populations in lakes and rivers with important ecological value or removing them from waterbodies where no socio-economic demands justify maintaining exotic species. No doubt, a comprehensive framework based on species and environmental-factor relationships, along with more detailed inventories, is still needed in Patagonia to promote native fish species conservation and develop sound management guidelines for exotic species.

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